

A NEW INVASION INTO AN ANCIENT LAKE – THE INVASION HISTORY OF THE DREISSENID MUSSEL *MYTILOPSIS LEUCOPHAEATA* (CONRAD, 1831) AND ITS FIRST RECORD IN THE CASPIAN SEA

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INTRODUCTION

The Ponto-Caspian region, which includes the Black, Caspian and Azov Seas, plays a major role as both a source (Ketelaars, 2004; Reid & Orlova, 2002) and recipient (Grigorovich et al., 2003) for biological invasions. Invasions from the Ponto-Caspian region are known to have had a considerably effect on the Baltic Sea and the North American Great Lakes (Reid & Orlova, 2002; Ricciardi & MacIsaac, 2000). Approximately 70% of the species that invaded the North American Great Lakes between 1985 and 2000 were originally endemic for the Ponto-Caspian region (Reid & Orlova, 2002). For example, 16 Ponto-Caspian macroinvertebrate species were found in coastal waters of the Baltic Sea, of these nine species were Crustacea, three species Mollusca, and three species Oligochaeta (Bij de Vaate et al., 2002).

Grigorovich et al. (2003) recorded species invasions into the Caspian Sea and identified 36 non-indigenous species (NIS) of invertebrates; of these 12 species were Crustacea, eight species Trematoda and six species Mollusca. Most NIS were introduced from the Atlantic-Mediterranean region (i.e., Lusitanian region of Atlantic Ocean, Mediterranean and Black Seas) (Grigorovich et al., 2003).

The Caspian Sea is the largest continental water body in the world. It has a surface area of approximately 400,000 km², a maximum depth of 1,025 m, and contains brackish water with a volume of almost 79,000 km³ (Dumont, 1998). It is structurally divided into three regions: Northern, Middle, and Southern Caspian with a salinity gradient ranging from 1–11 ppt in the northern to 12–13 ppt in the middle and southern part (Karpinsky, 1992). During summer the surface water temperature ranges from 24°C to 27°C and during winter from 0°C to 9°C (Reid & Orlova, 2002).

The Caspian Sea is believed to be the only extant lake formed from an ancient ocean (Riedel et al., 2006). The rate of endemism is high (Dumont, 1998; Kosarev & Yablonskaya, 1994). Endemic species in ancient lakes are often highly adapted to the conditions in their habitats and thus face higher risk when sudden changes in the ecosystems occur (Noges et al., 2008). Eutrophication and invasive species are two major threats to biodiversity in freshwater (Noges et al., 2008).

Often, when NIS arrive in the Caspian Sea, the invasion has already taken place in the Black Sea (de Mora & Turner, 2004). In 1952, the opening of the Volga-Don Canal facilitated the faunal exchange between the Caspian Sea and the neighboring Black Sea via the Don River and the Sea of Azov (Fig. 1). Shipping activities along the new invasion corridor even helped to increase the wave of introductions and became the major vector for NIS (Grigorovich et al., 2003). For example, the cirripedian crustaceans *Balanus improvisus* (Darwin, 1854) and *Amphibalanus eburneus* (Gould, 1841) established populations throughout the Caspian Sea after introduction from the Black Sea by ships via the Volga-Don Canal in the 1950s (Kosarev & Yablonskaya, 1994; Shiganova et al., 2005).

However, the Volga-Don Canal facilitates not only the immigration of exotic species to the Caspian Sea, but also the emigration of Caspian Sea species into other water bodies. One of the first mass invasions from the Ponto-Caspian region was caused by the biofouling zebra mussel *Dreissena polymorpha* (Pallas, 1771) (Bij de Vaate et al., 2002). The economic and ecological damage caused by altering ecosystems and displacing other species have been immense (Connelly et al., 2007; Karatayev et al., 1997). Similarly, the quagga mussel, *Dreissena rostriformis bugensis* Andrusov,

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TABLE 1. Invasion history of *Mytilopsis leucophaeata* (Conrad, 1831) in Europe.

Year of first record	Location	Source
1835	Antwerp, Belgium	Boettger (1928)
1895	Amstel River, The Netherlands	Maitland (1897)
1872	Northern France	Guerné (1873)
1928	Kiel Canal, Germany	Boettger (1932)
<1939	Kaliningrad Area, Russia	Zilch & Jaeckel (1962)
1993	Guadalquivir River, Spain	Escot et al. (2003)
1996	Cardiff Docks, South Wales, United Kingdom	Oliver et al. (1998)
1999	Thames River Estuary, E Coast, United Kingdom	Bamber & Taylor (2002)
2000	Warnow River, near Rostock, Germany	Darr & Zettler (2000)
2002	Black Sea Basin, Dniester Liman, Ukraine	Therriault et al. (2004)
2002	Canal Maritime, d'Aigues-Mortes, France	Girardi (2003)
2003	Loviisa Archipelago, Gulf of Finland	Laine et al. (2006)
2009	Southern Bug, near Mykolajiv, Ukraine	This study
2009	Caspian Sea, Iran	This study

1897 (other authors have given it species rank and treated it as *Dreissena bugensis*) from the Black Sea basin extended its range throughout wide parts of North America and more recently in western Europe (Martens et al., 2007; Molloy et al., 2007; Orlova et al., 2005). Our study focuses on invasion dynamics of another dreissenid, Conrad’s false mussel, *Mytilopsis leucophaeata* (Conrad, 1831),

(Bivalvia, Dreissenidae), which has moved into the Caspian via one or several routes. *Mytilopsis leucophaeata* is native along the southern coast of North America (southern USA to Tampico, Mexico) (Marelli & Gray, 1983), and with past known invasion into wide parts of North America and Western Europe, particularly the North Sea coast and several inland waters such as the Kiel Canal and Rhine

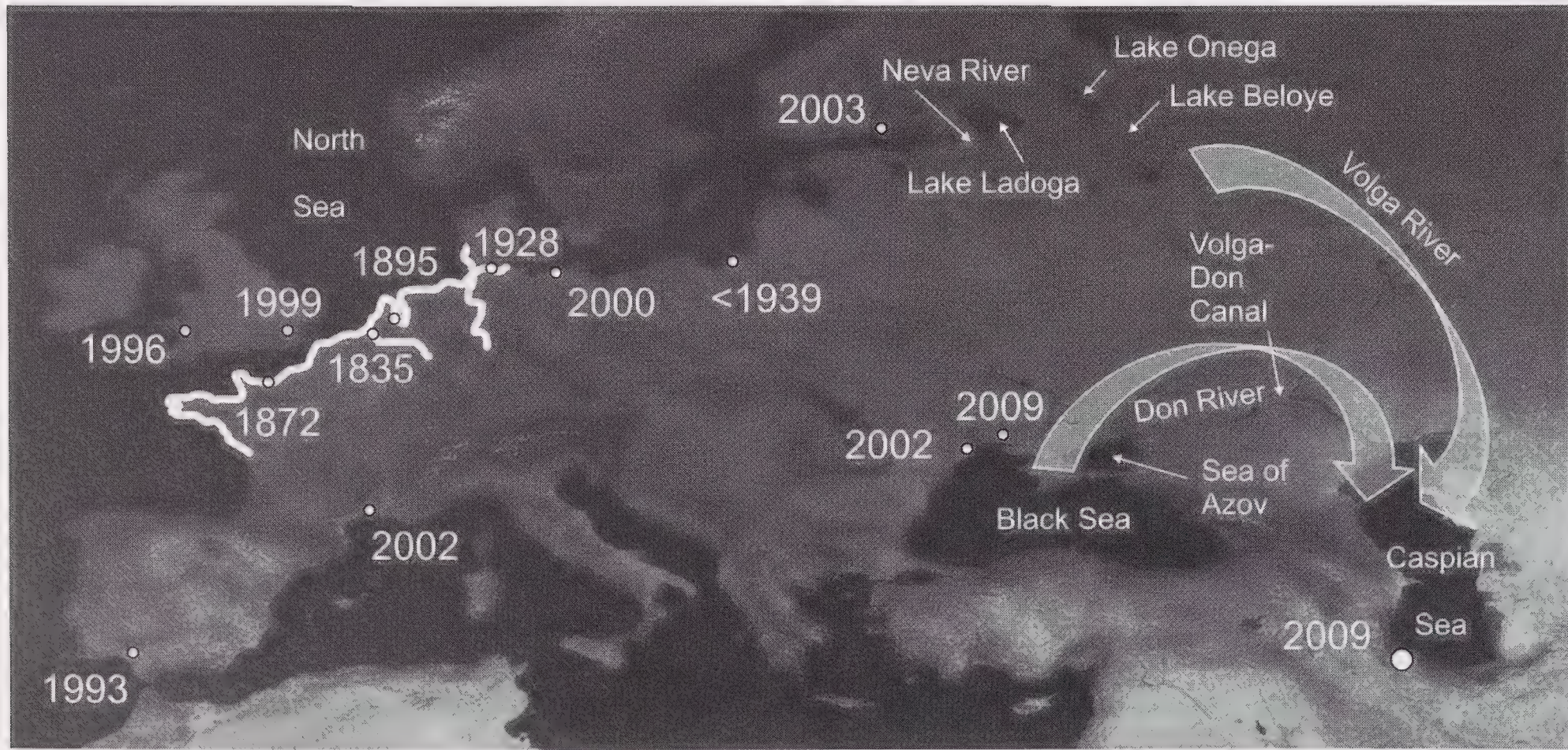


FIG. 1. Distribution of *Mytilopsis leucophaeata* (Conrad, 1831) (white line) and selected first records in Eurasia. The arrows indicate possible invasion routes into the Caspian Sea.

TABLE 2. Localities of sequenced individuals of *Mytilopsis leucophaeata* (Conrad, 1831), coordinates, and date of collection.

Location	Isolate/GenBank Accession #	Latitude (N) Longitude (E)	Date of Collection	Source
Belgium, Antwerp	5248/HM100251 5247/EF414477 11574/HM100252	51°21'34.99" 4°17'29.98"	19 Jan 2006	This study/ Albrecht et al. (2007)
Germany, Kiel Canal, near Baltic Sea	9984/HM100253	54°21'46.39" 9°49'09.68"	21 Oct 2008	This study
Germany, Kiel Canal, Brunsbüttel, near North Sea	9989/HM100254	53°54'36.77" 9°10'43.23"	20 Oct 2008	This study
Ukraine, Southern Bug, near Mykolajiv	12396/HM100255	46°58'49.26" 31°58'04.04"	3 Jul 2009	This study
Iran, Caspian Sea, Bandar Anzali	11313/HM100256 11314/HM100257 11317/HM100258 11572/HM100259 11573/HM100260 11788/HM100261 11794/HM100262	37°28'54.97" 49°27'37.01"	28 Apr 2009	This study
North America, Hudson River near Piermont, New York	U47649	n.a.	n.a.	Baldwin et al. (1996)

River and Weser River (Boettger, 1932; Jungbluth, 1996; Girardi, 2003; Therriault et al., 2004) (summarized in Fig. 1, Table 1). Like *D. polymorpha* and *D. r. bugensis*, *M. leucophaeata* has become a serious biofouling species in industrial pipe systems (Jenner et al., 1998; Rajagopal et al., 2002, 2005; Verween et al., 2005). It also has ecosystem engineering impacts similar to those of the zebra mussel (Pathy & Mackie, 1993; Sousa et al., 2009). Free-living planktonic larvae and high fecundity of dreissenids in general facilitates the transfer into new habitats and fast colonization (Bij de Vaate et al., 2002).

In 2002, it entered the Black Sea basin (Dniester Liman, Ukraine) (Therriault et al., 2004) and in 2003 the Loviisa archipelago, Gulf of Finland (Laine et al., 2006). These localities represent the most eastwards occurrences. In the Caspian Sea, there have been no records of this brackish water mussel until now.

MATERIAL AND METHODS

In April 2009, sampling to collect dreissenids took place in the southern part of the Caspian Sea from piers at a bridge in Bandar Anzali, Iran

(Table 2) by A. R. Mirzajani and S. Rahim from the Inland Waters Aquaculture Institute. The bridge is located between brackish (Caspian Sea) and freshwater environments (mouth of the Sefid River) where many cargo boats and ships offload ballast water. The sampling was done by hand or with a dip net down to approximately 1 m depth. Specimens of bivalves and associated fauna were stored in 96% ethanol for further morphological and molecular examination. DNA, shell and soft tissue vouchers have been archived in the collection of the Department of Animal Ecology & Systematics at the Justus Liebig University of Giessen (UGSB). DNA from seven bivalves was isolated using protocols of Winnepenninckx et al. (1998) and Wilke et al. (2006). For amplification, the mitochondrial cytochrome oxidase c subunit I (COI) gene with a target length of 655 bp was used (Folmer et al., 1994). Primers were utilized for amplification and sequences were produced with a LI-COR (Lincoln, Nebraska) Long ReadIT 4200 sequencer and the Thermo Sequenase Fluorescent Labelled Primer Cycle Sequencing kit (Amersham Pharmacia Biotech, Piscataway, New Jersey). Sequences were compared with available sequences from NCBI GenBank and with sequences from specimens

sampled in 2006, 2008 and 2009 from the invaded areas in Belgium and Germany and the Ukraine (Table 2). All sequences have been sent to NCBI GenBank (Table 2: GenBank accession numbers).

For morphological determination, the shell was opened to examine the internal structure. The shell length of 60 individuals was measured with a calliper and the fouling rate (i.e. number of balanid specimens per shell) was calculated.

RESULTS

During the sampling in spring 2009 in the Southern Caspian, several hundred dreissenid specimens were found with encrusting cirripedian crustaceans. The estimated biomass of bivalves and balanids was approximately 3 kg per m², while the abundance of individual balanids exceeded number of the bivalves (73% balanids and 27% bivalves). The water temperature was 18°C, the average pH value in this area in spring was 7.9,

and the average of the dissolved oxygen in spring was 8.9 mg/l. The shell morphological analysis of several mussel specimens from the Caspian Sea showed the existence of an apophysis on their myophore plate, which is present in *Mytilopsis leucophaeata* (Fig. 2), but absent in quagga or zebra mussels (Pathy & Mackie, 1993).

The COI sequences obtained confirmed the determination of this species as *M. leucophaeata*. The comparison of the COI sequence (528 bp) of seven individuals with *M. leucophaeata* from Germany (Kiel Canal), Belgium (Antwerp), Ukraine (Southern Bug), and North America (Savannah River, Georgia and Hudson River near Piermont, New York (GenBank: U47649)) (Table 2) revealed the presence of a single identical haplotype at all sites mentioned.

Shells sizes ranged from 5.5–22 mm (average 13.5 mm, n = 60). Thirteen of 60 specimens of *M. leucophaeata* examined were overgrown with *Amphibalanus eburneus* (Cirripedia). A maximum of five specimens of *A. eburneus* were found on one shell. Only mussels larger than 12.8 mm were overgrown.

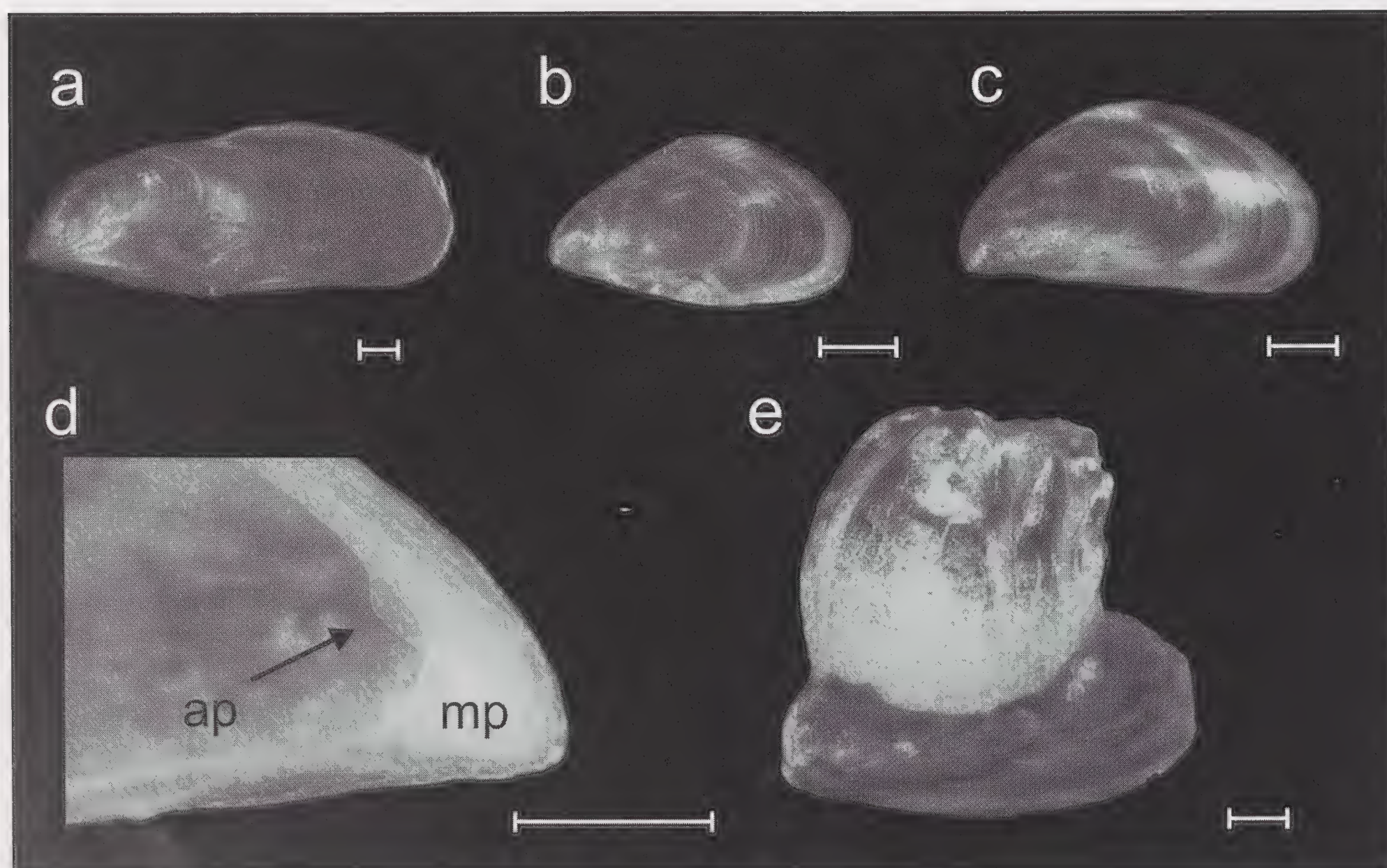


FIG. 2. Plate with three individuals of *Mytilopsis leucophaeata* (Conrad, 1831) from the Caspian Sea (11313 (a), 11573 (b), 11314 (c)), inner shell showing the apophysis (ap) of the myophoreplate (mp) (d) and *M. leucophaeata* overgrown with an individual of *Amphibalanus eburneus* (Gould, 1841) (e). Scale bar = 2 mm respectively.

DISCUSSION

Mytilopsis in the Caspian Sea

The population of *Mytilopsis leucophaeata* found in the Caspian Sea contained adult individuals with a maximum shell length of 22 mm. Verween et al. (2006) found the same maximum shell length in populations of *M. leucophaeata* in Belgium. Based on size, they calculated a longevity of greater than five years for this species. Thus, we assume that the larger individuals found in the Caspian Sea are approximately five years old and thus invaded the lake probably not later than 2004. Given the high densities we found and the fact that this population is at the far opposite end of the sea from the supposed entry point (Volga River Liman), it is likely that the first individuals might have invaded the Caspian Sea earlier.

The family Dreissenidae has been proposed to have originated in the Eocene, with a major radiation occurring in the Parathethyan Basin (today Black Sea, Caspian Sea, and Aral Sea) from the Late Miocene to the Pliocene (Starobogatov, 1994). While some species within this family are highly endemic, others have recently undergone a global redistribution, as summarized in Orlova et al. (2005). Transfer via shipping activities by means of transport as larvae in ballast water or as adults attached to ships' hulls with byssal threads seems to be responsible for the introduction of populations of *M. leucophaeata* from North America into Europe (Bamber & Taylor, 2002; Oliver et al., 1998) and was also presumed to be the case for the Black Sea (Therriault et al., 2004).

Canal construction, such as the Volga River system connecting the Caspian and Black Seas and the Baltic Sea, can serve as new invasion corridors for NIS overcoming physiological barriers (Reid & Orlova, 2002). The deletion of such barriers can have great impact on the endemic taxa by allowing the transfer of NIS between formerly isolated ecosystems (Therriault et al., 2004). This contact may cause competition between natives and endemics which may even lead to exclusion of the less competitive species (Albrecht et al., 2009).

The Caspian Sea mollusk fauna is mainly endemic and numerically dominated by cardiid and dreissenid bivalves and hydrobioid snails. Although the taxonomy of the Caspian Sea mollusk fauna is still not satisfactorily resolved (Wesselingh, 2007), several dreissenid taxa have been recognized. While Rosenberg &

Ludyanskiy (1994) distinguish four dreissenid taxa in the Caspian Sea on the basis of morphology and salinity tolerance: *D. polymorpha*; *D. rostriformis* Deshayes, 1838; *Dreissena elata* Andrusov, 1897; and *Dreissena caspia* Eichwald, 1855, other authors split *D. polymorpha* and *D. rostriformis* into several subspecies based on differences in depth at which they occur (reviewed in Rosenberg & Ludyanskiy, 1994). The invasive dreissenid *D. r. bugensis* has recently invaded the northern Caspian Sea where the Volga River dilutes the salinity to 2 to 3 ppt (Orlova et al., 2004). While *D. r. bugensis* has an upper salinity tolerance limit of 7 ppt (Oliver et al., 1998), *M. leucophaeata* is more euryhaline, being able to survive in salinity ranging from 0.1 to 31 ppt (Verween et al., 2007). In its native region, *M. leucophaeata* is present in warm, temperate waters (Marelli & Gray, 1983), but this species may occur also in water bodies with much lower temperatures (e.g. in the Kiel Canal in Germany). However, these permanent populations of *M. leucophaeata* in Europe remain rare due to variations in salinity or too low temperatures during winter – for example, for the UK (Eno et al., 1997), for parts of the coastal region in Europe (Wolff, 2005), for the Kaliningrad area (Darr & Zettler, 2000), and for Weser River (Bäthe, 1996). Thus, the southern Caspian Sea might much better comply with the requirements of this species (12–13 ppt and 9°C in winter). Given this fact, we suppose that *M. leucophaeata* has the ability not only to establish permanent populations but also invade further parts of the Caspian Sea or might already be present there. During the sampling no other dreissenid specimens were found, indicating that in this part of the Caspian Sea *M. leucophaeata* exceeded far the numbers of endemic dreissenids and is the dominant species.

Invasion Route

The broad ecological tolerance of *Mytilopsis leucophaeata* led Therriault et al. (2004) to conclude that *M. leucophaeata* has the ability to spread throughout the Ponto-Caspian region. Although it is possible that in exceptional cases dispersal events of aquatic mollusks can occur over land via bird migration (e.g., Haase et al., 2010), dispersal via waterways is more likely. Two main invasion corridors are suggested to have been the routes for the invasion in the Caspian Sea: as this species was already present in the Black Sea basin in 2002, this

bivalve may have been transported by ships via the Volga-Don Canal (Fig. 1). However, as established populations of *M. leucophaeata* in the Gulf of Finland were already recorded in 2003 (Laine et al., 2006), it could be also possible that this bivalve arrived in the Caspian Sea via the Volga River (Fig. 1). This invasion corridor includes long-distance larvae dispersal via the Baltic Sea, Neva River, Lake Ladoga, Lake Onega, Lake Beloye and Volga River (Fig. 1). This invasion corridor is one of the three invasion routes that Bij de Vaate et al. (2002) hypothesized for NIS emigrating out of the Ponto-Caspian region. However, it is also conceivable that NIS may enter the Ponto-Caspian region using these corridors. To clarify the question of the invasion route satisfactory, molecular studies including a more variable marker should be conducted.

The COI-gene has been shown to be very informative for population genetics in Balkan endemic dreissenids *D. blanci* Westerlund, 1890 and *D. presbensis* Kobelt, 1915, which are characterized by a high degree of variability (Wilke et al., submitted). However, in the invasive dreissenids *D. polymorpha* and *D. r. bugensis*, the invading populations show a low genetic variability in COI, presumably resulting from bottlenecks during invasion (May et al., 2006; Albrecht et al., in prep.). Despite the lack of genetic differentiation in invading dreissenids, founding populations seem to be very successful. While the low genetic differentiation among populations in the invaded range of *M. leucophaeata* is thus not surprising, it would be interesting to examine the genetic structure in their native region.

Conservation Issues

The biodiversity of the world's ancient lakes is threatened by a variety of anthropogenic factors: introduction of invasive species, pollution and fishing activities are only some of the reasons why aquatic ecosystems have rapidly changed and extinction rates have increased dramatically (Cohen, 1994). Caspian biodiversity is threatened by two major kinds of human activities: (1) shipping transfer and connection of previously separated water systems, which has introduced NIS, and, (2) impairment in the water quality caused, for example, by oil exploitation and pollution (Stanners & Bourdeau, 1995). These dual threats work synergistically and may amplify impacts on the native fauna.

The Middle and Southern Caspian are particularly at risk, where decreasing species

diversity of phytoplankton, zooplankton and macrobenthos has been reported (summarized in Stanners & Bourdeau, 1995). Other authors have already presumed the extinction of *Dreissena caspia* and *D. elata* following the invasion of *Mytilaster lineatus* (Gmelin, 1791) (Rosenberg & Ludyanskiy, 1994) and suggested that the invasion of *M. leucophaeata* may herald a further loss of native bivalves in the Black Sea (Therriault et al., 2004).

Because of its demonstrated high colonization success, ecosystem engineering impacts and tendency to dominate the fauna, this new invasion of *M. leucophaeata* is likely to pose a serious further threat to the endemic dreissenid fauna in the Caspian Sea.

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